Obstacle avoidance during human walking: H-reflex modulation during motor learning

Hess, F ; van Hedel, H J A ; Dietz, V

Abstract: The goal of this study was to investigate changes of H-reflex amplitudes during a motor learning task. Subjects with reduced vision were instructed to step over an obstacle on a treadmill as low as possible, while the soleus H-reflex was elicited. Acoustic warning and feedback signals about performance were provided. Performance improvement was associated with a decrease of muscle activity, needed to step over the obstacle (rectus femoris, biceps femoris, tibialis anterior and gastrocnemius medialis muscles), and of foot clearance, while joint angle trajectories from knee and ankle became more stable. The experiment consisted of five runs, three with normal treadmill walking and two with randomly stepping over the obstacle (100 times). H-reflexes were elicited at early and late stance phase before stepping over the obstacle. H/M ratio, latency and duration were determined. The values of these measures were calculated for the onset and end of a run and their course over time was evaluated using a correlation coefficient. The largest adaptations with a significant increase of reflex amplitude occurred during the first obstacle run. This increase lasted only briefly and the reflex amplitudes decreased to their previous values. During the later obstacle run, no H-reflex modulation occurred. It is concluded that a motor learning task causes adaptational effects not only on performance, but also on H-reflex responses. The results indicate that most of the modulation of H-reflexes is probably due to supraspinal influences on reflex transmission. The observations made are probably less specific for this motor task (stepping over the obstacle), but rather associated with the increased attention required by the motor learning task during the first obstacle run

DOI: https://doi.org/10.1007/s00221-003-1415-7

Exp Brain Res (2003) 151:82–89
DOI 10.1007/s00221-003-1415-7

RESEARCH ARTICLE

F. Hess · H. J. A. van Hedel · V. Dietz

Obstacle avoidance during human walking: H-reflex modulation during motor learning

Received: 20 June 2002 / Accepted: 21 January 2003 / Published online: 14 May 2003

Abstract The goal of this study was to investigate changes of H-reflex amplitudes during a motor learning task. Subjects with reduced vision were instructed to step over an obstacle on a treadmill as low as possible, while the soleus H-reflex was elicited. Acoustic warning and feedback signals about performance were provided. Performance improvement was associated with a decrease of muscle activity, needed to step over the obstacle (rectus femoris, biceps femoris, tibialis anterior and gastrocnemius medialis muscles), and of foot clearance, while joint angle trajectories from knee and ankle became more stable. The experiment consisted of five runs, three with normal treadmill walking and two with randomly stepping over the obstacle (100 times). H-reflexes were elicited at early and late stance phase before stepping over the obstacle. H/M ratio, latency and duration were determined. The values of these measures were calculated for the onset and end of a run and their course over time was evaluated using a correlation coefficient. The largest adaptations with a significant increase of reflex amplitude occurred during the first obstacle run. This increase lasted only briefly and the reflex amplitudes decreased to their previous values. During the later obstacle run, no H-reflex modulation occurred. It is concluded that a motor learning task causes adaptational effects not only on performance, but also on H-reflex responses. The results indicate that most of the modulation of H-reflexes is probably due to supraspinal influences on reflex transmission. The observations made are probably less specific for this motor task (stepping over the obstacle), but rather associated with the increased attention required by the motor learning task during the first obstacle run.

Keywords Obstacle avoidance · Motor control · Motor learning · H-reflex · Adaptational effects

F. Hess · H. J. A. van Hedel (✉) · V. Dietz
Balgrist University Hospital, Spinal Cord Injury Center,
Forchstrasse 340, CH-8008 Zürich, Switzerland
e-mail: hvanhede@balgrist.unizh.ch
Tel.: +41-1-386 37 28
Fax: +41-1-386 37 31

H. J. A. van Hedel
Catholic University Nijmegen,
Department of Medical Physics & Biophysics,
Nijmegen, The Netherlands

Introduction

When stepping over an obstacle, subjects subconsciously make adaptations to perform the motor skill. The central nervous system (CNS) automatically develops strategies to maintain body equilibrium and to adapt the locomotor pattern to the actual requirements. When subjects step over obstacles, usually vision is used for control in a feedforward manner (Patla and Vickers 1997). Hip, knee and ankle joints become more flexed (Patla and Prentice 1995), while intersegmental dynamics are used to simplify the movement over the obstacle and minimise energy costs. While these adaptations are controlled by supraspinal structures, spinal structures are involved as well to preserve balance and to ensure stable walking pattern movements throughout the step cycle (Zehr and Stein 1999; for review see Dietz 1997).

Spinal reflex mechanisms play a major role during: (1) the acquisition and (2) the maintenance of new locomotor skills (for review see Wolpaw and Tennissen 2001). (1) Evidence that motor learning involves spinal neuronal circuits came from investigations on spinalised cats, which were task specifically trained to stand or to step on a treadmill (De Leon et al. 1998; Edgerton et al. 1992). Furthermore, in humans with a complete spinal cord injury, task appropriate changes in leg muscle electromyographic (EMG) activity were seen after regular training on a treadmill (Dietz et al. 1994).

(2) Evidence that spinal reflex mechanisms have a function in maintaining locomotor skills came for example from a study showing that both H-reflex and disynaptic reciprocal inhibition were stronger, when healthy adults were more physically active than controls (Nielsen et al. 1993). However, in ballet dancers, who

were the most active, the H-reflexes were the lowest. It was speculated that small reflexes might allow an enhanced cortical control and, consequently, precise movement performance (Nielsen et al. 1993).

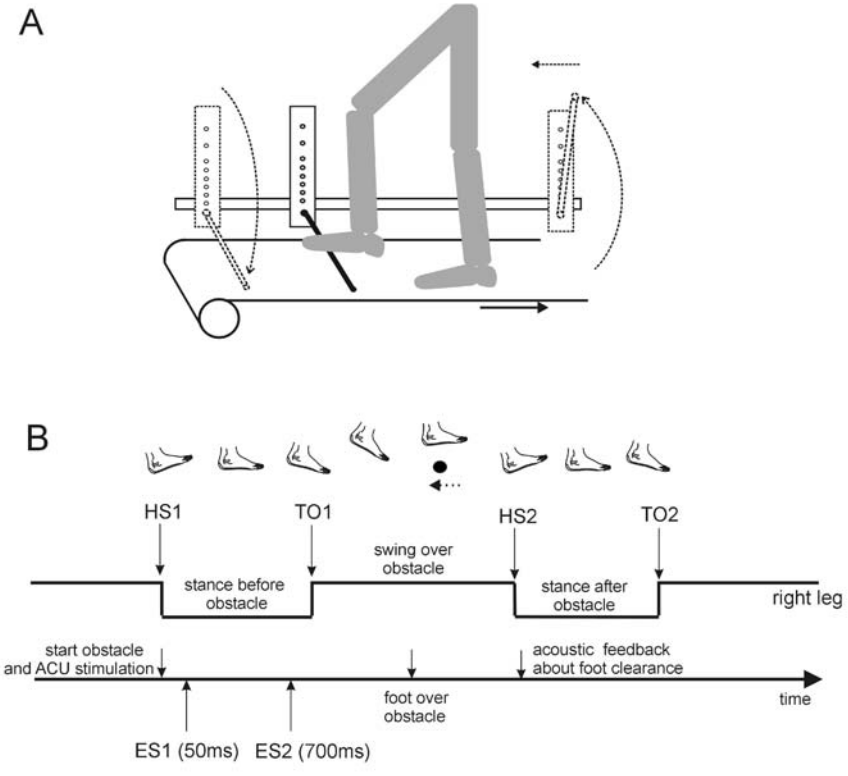
In a recent study, it was proposed that stepping over an obstacle involves supraspinal centres like the brainstem (Van Hedel et al. 2002). Such an involvement might be associated with changes in the transmission in spinal pathways. In this study, H-reflexes were used as an assessment tool to investigate possible changes in spinal segmental pathway transmission. The aim was to evaluate how far the adaptational changes caused by repetitive obstacle stepping are reflected in a modulation of the H-reflex in healthy subjects. It is hypothesised that modulation of the reflex size occurs during adaptation to the new motor task.

Material and methods

General procedures and recording methods

The experiments were performed with approval of the local Ethics Committee. All subjects gave written informed consent. The experiments were run in accordance with the Declaration of Helsinki. The nine subjects, aged between 23 and 37 years, had no signs of neurological, orthopaedic or cardiovascular disease. Subjects with a body mass index higher than 30 were excluded.

Throughout the experiment the subjects walked on a treadmill (Woodway, Weil am Rhein, Germany). A custom-built obstacle machine was placed next to the treadmill (Fig. 1) in order to study repetitive stepping over the obstacle. The obstacle consisted of a foam stick 11 cm above the treadmill. It was attached to the obstacle machine in such a way that it folded back with the slightest touch. It caused no perturbations in the movement. The force signal of the force plate located underneath the right belt (in front of the position of the subject) was used as a trigger to start the obstacle machine. The impact of the right foot, i.e. heel strike (HS1), was used to start the movement of the obstacle. At this time, a short acoustic beep of 100 ms duration warned the subject of the starting obstacle (Fig. 1). The time between obstacle steps varied randomly between 10 and 16 s, i.e. 6–11 normal gait cycles. After release, the obstacle moved with the same speed as the treadmill and the subject could step over the obstacle without changing the rhythmic walking



C

Sequence of conditions

Run	Task
1	Normal treadmill walking
2	Normal treadmill walking
3	Stepping over obstacle 100 times
4	Stepping over obstacle 100 times
5	Normal treadmill walking

Fig. 1 A Experimental set-up. The obstacle machine was placed next to the treadmill and moved with the same speed as the treadmill. At the end of the treadmill the obstacle folded up and moved back to its starting position. Eight light sensitive diodes detected foot clearance. **B** Timing of events. The obstacle machine and the acoustic (*ACU*) warning signal were released by first heel strike (*HS1*). H-reflex stimulation occurred 50 ms (*ES1*) or 700 ms (*ES2*) after HS1. After the swing phase over the obstacle, the acoustic feedback signal, indicating foot clearance, was provided. RMS of leg muscle activity and variation ratio (*VR*) of joint angle trajectories were calculated between first toe-off (*TO1*) before the swing over the obstacle and second toe-off (*TO2*). **C** Sequence of conditions (all were performed with reduced vision)

cadence. After the subject stepped over the obstacle, it folded up and moved back to its starting position.

The subjects had reduced visual input, due to special glasses that prevented visual information about the obstacle and the treadmill. A previous study showed that more learning occurred in the situation where subjects had reduced vision and received acoustic feedback compared to the situation where subjects had full vision (Erni and Dietz 2001). Small earplugs provided warning and feedback signals as well as 'rainy' noises in the background. Additionally, the subjects wore a headphone over the earplugs, which eliminated all acoustic information about movement of the obstacle machine.

When the subject stepped over the obstacle the level of foot clearance was determined by a vertical linear array of eight light sensitive diodes that were attached to the obstacle machine above the foam stick. The lowest diode was placed 2 cm above the obstacle and the distance between each diode was 2 cm (3 cm for the upper two diodes, Fig. 1). The signal of the lowest activated diode was recorded for each step over the obstacle and the subject received the corresponding acoustic feedback signal. The higher the foot clearance, the higher the feedback signal. When the lowest diode was activated (optimal foot clearance) a double beep (707- and 1400-Hz sinusoidal signals, 600 ms duration) was activated. The other feedback signals consisted of a single beep (125-, 176-, 250-, 354-, 500-, 707- and 1000-Hz rectangular signals of 400 ms duration for the second lowest to the highest diode, respectively). Before the experiment started, the volunteers received instructions and were familiarised with the approach. They stepped five times over the obstacle with full vision and both acoustic signals (warning and feedback).

Data recording and analysis

EMG recordings were made using surface electrodes from the rectus femoris (RF), biceps femoris (BF), gastrocnemius medialis (GM), tibialis anterior (TA) and soleus (SOL) muscles of the right leg. Ankle and knee joint movements of the right leg were monitored using mechanical goniometers fixed at the lateral aspect of each joint.

The general recording technique and the data analysis have been described in detail previously (Dietz et al. 1995; Erni and Colombo 1998). Briefly, the EMG signals were amplified, band-pass filtered (30–300 Hz) and transferred together with the biomechanical signals to a PC system via an analog-to-digital converter. All signals were sampled at 1000 Hz. The EMG signals were rectified. For the evaluation of changes in leg muscle EMG activity from the first to the last step over the obstacle within a run, the signal energy (root mean square, RMS) was determined for each step cycle for an interval between first toe-off (toe-off before onset of the swing over the obstacle or TO1) and second toe-off (TO2; see Fig. 1).

For the same interval, the variation ratio (VR) for each joint movement signal was calculated to analyse changes in the leg's trajectory over the obstacle within each run. The VR provides a measure of the similarity of several waveforms (Erni and Colombo 1998). Here the VR was calculated between two trajectories. First, the mean trajectory of the last three steps of a run was calculated, i.e. when the leg movement was stabilised. Then, the movement trajectory of each step was compared with this mean using the VR. For completely reproducible waveforms the VR tends to zero; for dissimilar waveforms the VR tends to one.

Analysis of obstacle experiment data

Motor learning was reflected in an improvement of motor performance. A better performance occurred when: (1) the RMS values for leg muscle activation became smaller (Erni and Colombo 1998), as well as (2) the VRs of the joint movement signals and (3) the level of foot clearance over the obstacle.

The various measures were also analysed for runs 1, 2 and 5 (normal treadmill walking), except for the measure of foot clearance. The latter could not be recorded since the light diodes were attached above the obstacle machine, which was too high to record foot clearance during normal walking (Fig. 1).

The course over time was evaluated using a correlation coefficient (CC). The measures were normalised by dividing each value by the mean calculated per run and subject. The measures were logarithmically transformed and Pearson's CC r was calculated between the number of steps recorded (runs 1, 2 and 5) or the number of steps over the obstacle (runs 3 and 4) and the measures using the normalised and logarithmically transformed data for each run and each subject. Mean correlation coefficients (CCs) were calculated for all subjects using Fisher's Z-transformation.

Differences in CCs between the different runs were analysed using repeated measures analysis of variance (ANOVA) and a Bonferroni correction. The optimal covariance structure was determined using Akaike's information criterion and Schwarz's Bayesian criterion. The measure foot clearance was tested using a paired t-test.

Analysis of H-reflex modulations

Electrical stimuli were applied to the tibial nerve in the fossa poplitea to elicit the H-reflex using surface electrodes. H-reflexes were elicited using an electrical bipolar square pulse of 3 ms duration. The cathode was placed in the popliteal fossa, the anode just above the patella. Maximal M-wave (Mmax) was determined in a static condition. Subjects stood in a relaxed position, while electrical stimuli were applied to the tibial nerve with intervals of 2 s. Electrical stimulus strength was increased in steps of 0.8 mA. H-reflex and M-waves were recorded depending on the stimulus strength seven times on each level. Maximum H-reflex (Hmax) and Mmax were calculated by averaging the seven plotted H-reflexes of each level. To ensure that the stimulus strength was applied to the increasing slope of the H-reflex amplitude, the strength was reduced by 10%.

H-reflexes were elicited during the stance phase, before the subject had to step over the obstacle. The reflexes were elicited during the early stance phase, 50 ms after HS1 (electrical stimulation 1; ES1) and late stance phase, 700 ms after HS1 (ES2). Step cycle duration was set at 1.5 s. The treadmill speed was adapted accordingly and varied between 2.0 and 2.6 km/h (mean ± SD: 2.34 ± 0.16 km/h). A constant cadence was achieved by using a metronome positioned right next to the subject's headphones. Subjects could hear the metronome well, without hearing the noises coming from the obstacle machine.

Peak to peak amplitude, latency and duration were calculated for both M-waves and H-reflexes. Peak to peak amplitudes of the H-reflexes were normalised by dividing H-reflex amplitudes by Mmax elicited in the static condition (H/M ratio). Analysis was performed when a clearly defined H-reflex or M-wave or both were found. Measurements of an H-reflex without M-wave or vice versa were used and not eliminated. An H-reflex without M-wave can be explained by a stimulus strength below the motor threshold of the M-wave. Stimuli without any response (M-wave/H-reflex) were not included in the further analysis.

Onset and end H/M ratio levels were calculated by averaging the first and the last four H/M ratios, respectively, for each subject per run. Differences in levels were analysed between onset and end values of one run and between end and onset values of successive runs, e.g. the end value of run 2 and the onset value of run 3. Differences were tested using paired t-tests.

Corresponding to the performance measures, the course over time was analysed by calculating Pearson's CC r between the number of steps (runs 1, 2 and 5) or the number of steps over the obstacle and the H-reflex measures. H-reflex latency and duration were first normalised for each run and each subject by dividing them by their mean. All measures were logarithmically transformed. Mean CCs were calculated for all subjects using Fisher's Z-transformation.

Again, differences in CCs between the runs were analysed using repeated measures ANOVA, the structure of which was selected

using Akaike's information criterion and Schwarz's Bayesian criterion, and a Bonferroni correction.

The whole experiment consisted of five runs (Fig. 1). Between each run, the subjects had a break of 3–5 min. In the first two runs and the last run, subjects performed normal treadmill walking wearing the glasses and earphones. H-reflexes were elicited, 25 at early stance and 25 at late stance. The order of early (ES1) and late (ES2) stimuli varied sequentially, starting with an early stimulus. During runs 3 and 4, subjects stepped 100 times over the obstacle. During these runs, 50 H-reflexes were elicited during the early stance phase and 50 in the late stance phase.

Control experiments

Control experiments were performed in two subjects to investigate whether a general focus on learning a new motor task could be the reason for possible differences in H/M ratios between the runs or whether these differences were due to this specific motor learning task, i.e. stepping over the obstacle. The experiments were performed under the same conditions (reduced vision and acoustic warning and feedback signals). After one control run with normal treadmill walking, subjects performed two experimental runs with stepping over the randomly approaching obstacle. Again, the interruption between these runs was 3–5 min. The obstacle approached randomly between 10 and 16 s. H-reflexes were also elicited during normal walking steps performed between the obstacle steps. Again, the reflexes were released 50 and 700 ms after HS1. It was hypothesised that if a more general focus on learning a new motor task caused differences in H-reflex responses, there would be no differences between the H-reflexes elicited in both conditions. When differences occurred, changes in H-reflex responses would indicate specific changes related to the obstacle task.

Results

Runs 1, 2 and 5 were performed without stepping over the obstacle. During these runs 50 H-reflexes were elicited and the steps were analysed similar to runs 3 and 4, where subjects had to step 100 times over the obstacle and 100 H-reflexes were recorded. Negative CCs indicate a decrease of the measure over the number of steps.

H-reflex modulation during early stance

Figure 2 shows a representative individual example of the changes occurring in the peak to peak amplitude of H-reflexes when a subject performed normal stepping movements on the treadmill or stepped repetitively over the obstacle. CC calculated for the normalised and logarithmically transformed data ($r_{log\text{-}log}$) are displayed next to the slope (A) as well as the absolute value of the peak to peak amplitude. Additionally, the slopes of four averaged H-reflex responses, i.e. the first (B) and last (C) four H-reflexes of this run, are shown.

In general H/M ratios were relatively low, due to the low background activation level of the SOL in these phases of the step cycle. All M-wave data were constant throughout all runs, including the peak to peak amplitudes. Recordings without H and M responses occurred rarely, usually during late stance phase, randomly distributed over the run.

As expected, the CCs of the H/M ratio were in general low during runs 1, 2 and 5 (r = 0.137, 0.199 and 0.153 respectively). The CC of run 4 was also low, but negative (r = −0.119). Run 3 showed the highest, negative CC of −0.249. Repeated measures ANOVA showed a significant difference between the runs (P<0.01). Comparisons between the runs separately, using the Bonferroni correction, showed significant differences between the CCs of runs 3 and 1, 2 and 5 (for all P<0.05). There was no significant difference between the CCs for the measures latency and duration.

The levels of the H-reflex amplitudes at onset and end are shown in Fig. 3. The average level of the H/M ratio at the onset of the first run was 0.052; the end level was 0.079. In run 2, the onset level was 0.065; the end level was 0.054. Run 3 started significantly higher compared to run 2 (H/M ratio = 0.092; P<0.01) and decreased significantly (H/M ratio = 0.049; P<0.05). The onset and end levels of run 4 were 0.073 and 0.068 respectively; for run 5 they were 0.067 and 0.072. The average onset latencies varied between 31.2 and 32.2 ms and the duration between 11.2 and 12.8 ms. No significant changes were found for both latency and duration of the H-reflexes.

H-reflex modulation during late stance

Similarly to during early stance, the largest CC was observed during run 3 (r = −0.187). The CCs calculated for runs 1, 2, 4 and 5 were −0.114, 0.094, −0.177 and −0.183, respectively. Repeated measures ANOVA showed a significant difference between the runs (P<0.01). Pairwise comparisons using Bonferroni's correction revealed a significant difference between runs 1 and 5 (P<0.05). There was no significant difference between the CCs calculated for the measures latency and duration.

When onset and end levels of the H/M ratio were compared (Fig. 3), the only significant difference existed between the end level of run 2 (value = 0.045) and the onset level of run 3 (value = 0.114; P<0.05). No further significant differences were detected. The averaged onset latencies varied between 31.2 and 32.1 ms and the duration between 11.2 and 12.4 ms. No significant changes were found in both latency and duration of the H-reflexes.

Furthermore, H-reflex amplitudes depend on the level of background EMG of the SOL. The H-reflexes were elicited at the onset and end of the stance phase (minimal SOL EMG activity), just before the step over the obstacle took place. Background SOL EMG was evaluated by calculating the RMS for the same time interval where the H-reflex responses were expected to appear, i.e. 50 ms and 700 ms after HS. The calculation was done for the steps where no H-reflexes were elicited in the early and late stance phase. No changes in background SOL EMG were found throughout the analysed runs (Fig. 3). Thus,

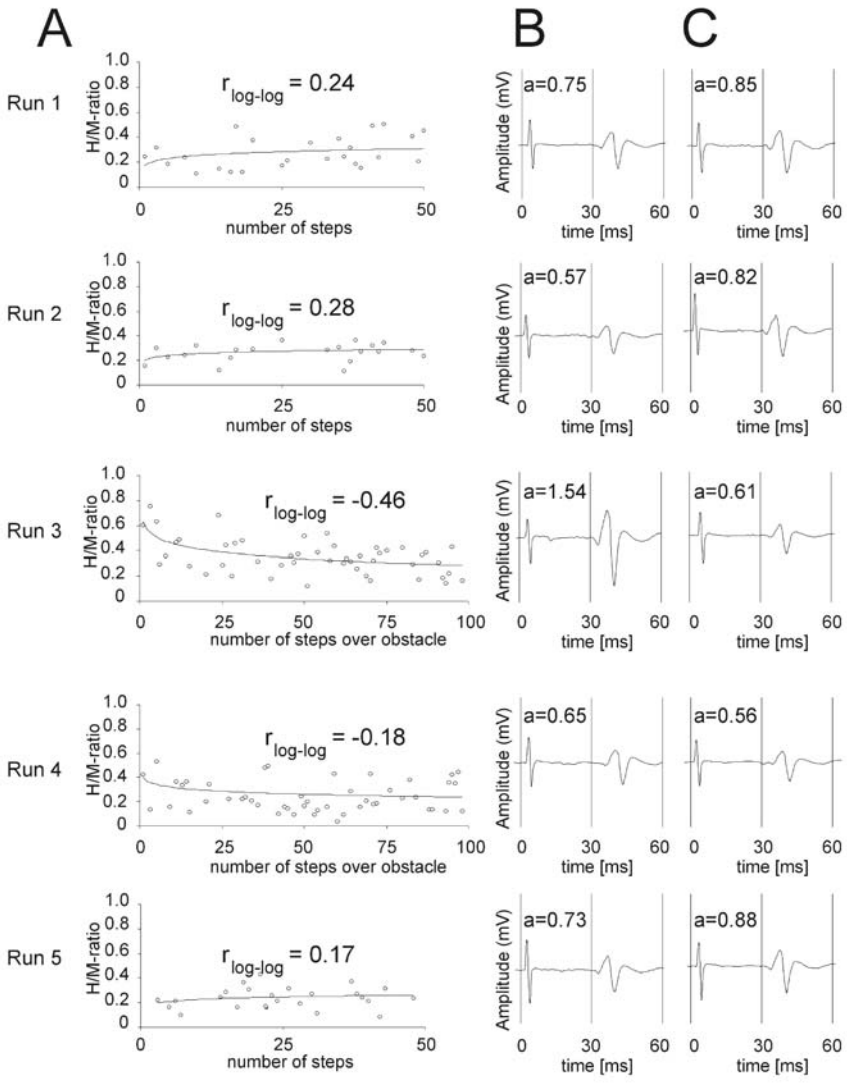


Fig. 2A–C H/M ratio of the H-reflex elicited 50 ms after heel strike of one subject for control runs (runs 1, 2 and 5) and for steps over the obstacle (runs 3 and 4). **A** Course of the H/M ratio calculated for the number of steps with fitted curve (power function). The correlation coefficients are displayed for the logarithmically transformed data ($r_{log\text{-}log}$). **B** and **C** are averaged curves of the first **(B)** and last **(C)** four curves recorded of the H-reflexes per run. The peak to peak amplitudes (*a*) are displayed in millivolts. Between 30 and 60 ms, the H-reflex responses appeared

changes in modulation of H-reflex responses can hardly be attributed to changes in background SOL EMG.

Obstacle experiment

The results of the obstacle experiment are shown in Fig. 4. Repeated measures ANOVA showed a significant difference between the CCs of all runs for the RF, while pairwise comparison with a Bonferroni's correction showed a significant difference between runs 3 and 5. The CCs calculated for the BF were significantly different between all runs, while runs 3 and 4 and runs 3 and 5 were also different in the pairwise comparison. There was no significant difference found for the TA (P=0.07) and the GM (P=0.31). For the ankle joint trajectories, a significant difference was found between all runs, although pairwise comparisons showed no significant difference. The adaptations in the knee joint trajectories differed between all runs, while pairwise comparison showed significant differences only between runs 3 and 1, 2 and 5. Furthermore, runs 3 and 4 differed significantly. A paired *t*-test showed a significant difference for the foot clearance between runs 3 and 4.

Control experiments

In a few control experiments possible differences in H-reflex modulation between normal and obstacle stepping were evaluated. No differences were found between the measurements in the two conditions within one run. There was no difference in H-reflex response between steps over the obstacle and normal steps.

Discussion

The aim of this study was to evaluate how far the adaptational changes caused by repetitive obstacle stepping were reflected in a modulation of the H-reflex in healthy subjects. Mean findings are that during repetitive

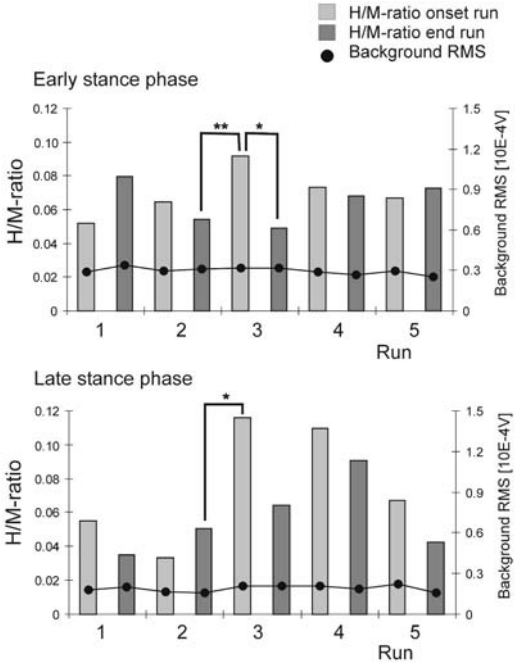


Fig. 3 Levels of the H/M ratios at onset and end of each run, as well as RMS values (in volts) calculated for the background EMG activity (*light grey* onset level of the run, *dark grey* end level of the run). **P*<0.05, ***P*<0.01

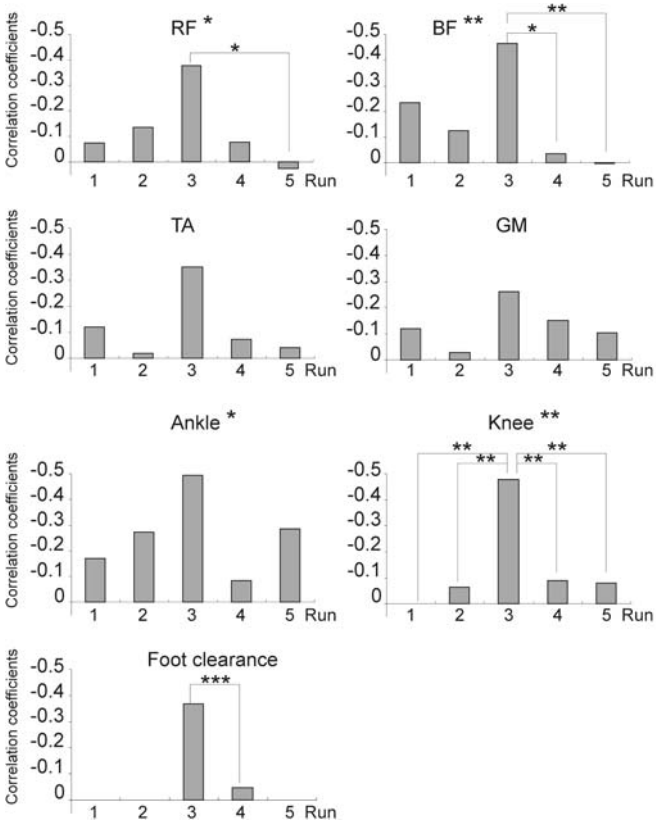


Fig. 4 Correlation coefficients calculated between the number of steps (over the obstacle in runs 3 and 4) and the different measures. *Asterisk* after a measure indicates a significant difference between all runs for that measure. **P*<0.05, ***P*<0.01, ****P*<0.001

stepping over an obstacle: (1) performance improves and (2) H-reflex modulation occurs in the early stance phase. It appears that the H/M ratio increases strongly when a motor learning task starts and reduces over the course of exercise.

Obstacle experiment

According to the study of Erni and Dietz (2001), the performance of stepping over the obstacle improves with repetition. The adaptational changes found (reduction in muscle activity, lower foot clearance and more stable leg movement trajectories) indicate that subjects adapted their walking pattern to a more economical and efficient way of stepping over the obstacle. None of these effects can be attributed to an increase of fatigue during the runs because there was no increase in obstacle hits (one to two per run; see also Erni and Dietz 2001).

All measures adapted significantly during the third run compared to other runs, except for the TA and GM EMG activity and the ankle joint trajectory. No differences were found between run 4 and the control runs. This indicates that the measures did not further improve during the second obstacle run, i.e. the subjects did not step over the obstacle in a more efficient way.

Methodological considerations

When the linear CC of the H/M ratio and its value at onset and end of run 2 were compared, a contrast can be seen. The fact that the end value was slightly smaller (0.054) than at the onset (0.065) would imply a negative CC. However, the CC was positive (CC = 0.199). This difference is probably due to the calculation method of both parameters. While the onset and end values were calculated by using only the first and the last four values of the 'raw' H/M ratio data, the CC was calculated between the number of steps and all H/M ratios using the normalised and logarithmically transformed data.

It was expected that modulation would occur for H-reflexes elicited in the late stance phase, i.e. 700 ms after HS1. However, while modulation of H-reflexes associated with learning clearly existed when elicited during the early stance phase, little modulation of H-reflex amplitudes was observed when elicited during late stance phase. Due to the fact that the warning stimulus was given at the onset of HS1, it was expected that if a task specific modulation occurred, 50 ms would be too short a period for the CNS to induce a H-reflex modulation.

One reason for the lack of H-reflex modulation during the late stance phase could be that the results were confounded by the influence of (small) differences in step length. Although subjects walked with the same cadence using the metronome, small differences in length and timing of (parts of) the step cycle cannot be excluded. Due to the normal modulation of the H-reflex (the H-reflex amplitude decreases strongly at the end of the

stance phase), relatively large differences in amplitude could be due to differences in the relative timing of H-reflex appearance.

Differences in H-reflex modulation associated with learning

In the present study, it was observed that adaptational changes caused by repetitive obstacle stepping are reflected in a modulation of the H-reflex in healthy subjects. This is in line with the literature that spinal reflex modulation is involved in learning and maintaining motor skills (Meyer-Lohmann et al. 1986; Myklebust et al. 1986; Nielsen et al. 1993). More comparable to the present study, it was suggested that adaptive changes observed during the acquisition of a specific locomotor task like hopping on one leg in different conditions or split-belt walking might be due to changes on a spinal level (Anstis 1995; Prokop et al. 1995).

The adaptational changes in H-reflex amplitude observed here can hardly be attributed to the acoustic warning signal indicating an obstacle trial. The short period of 50 ms between the warning signal and the enhanced reflex amplitude, combined with the result of the control experiment that within a run, the reflex amplitude was the same for normal and obstacle steps, indicate that the assessed changes are rather due to a more general focus on learning a new locomotor task. Such a supraspinal influence on spinal reflex behaviour is in line with suggestions made on H-reflex conditioning (Wolpaw 1997).

H-reflex modulation occurred with a short-lived increase of reflex amplitude at onset of the first obstacle run, and a strong decay during the initial adaptation to the new task. The H-reflex is frequently employed to reflect changes in spinal neuronal circuits (operant conditioning). During operant conditioning, subjects or animals become rewarded when reflex amplitudes are above (up-training) or below (down-training) a criterion value. H-reflex conditioning and motor learning as it occurs in normal life are closely linked with each other (Wolpaw and Tennissen 2001). Both H-reflex conditioning and learning can be attributed to a CNS plasticity at multiple sites. Operant conditioning of the H-reflex and of the stretch reflex has provided evidence of an activity-dependent spinal cord plasticity in rats (Chen and Wolpaw 1995), monkeys (Wolpaw et al. 1983) and humans (Evatt et al. 1989; for review see Wolpaw 1997). During conditioning, H-reflex amplitudes change over days and weeks.

This adaptation appears to occur in two phases in primates (Wolpaw and O'Keefe 1984): a small, rapid phase in the first few hours or days and a much slower second phase that continues for weeks. The first effect observed in the present study, i.e. the immediate increase in H-reflex amplitude at the onset of the first obstacle run, is suggested to correspond to this short first phase. These fast reflex modulations might be attributed to descending influence on the spinal reflex arc. In previous studies it was assumed that the corticospinal tract plays an essential role in this influence in rats (Chen and Wolpaw 1997; Chen et al. 2000), as well as in non-human primates (Wolpaw and Downmann 1988) and humans (Segal 1997). This plasticity might occur within spinal interneurons mediating presynaptic inhibition of Ia afferents (Wolpaw 1997) causing an immediate increase in H-reflex amplitudes at the onset of learning the new locomotor task.

The second effect observed in the present study, the decrease in H-reflex amplitude during the learning process, might reflect the descending influence during the course of motor learning. It might even be speculated that the newly acquired task, i.e. repetitive stepping over the obstacle, becomes successively automatically performed and controlled on a spinal or brainstem level. This stage might be reflected in the normalisation and stabilisation of the H-reflexes observed during run 4 and might correspond to the second, slower phase (Wolpaw 1997). It remains open for future studies investigating long-term obstacle stepping whether changes in H-reflexes in such a task can be associated with long-term changes in the excitability of spinal neuronal circuits.

Acknowledgements We thank C. Bastiaanse, I. Pappas, T. Keller and G. Colombo for their technical help. This work was supported by grants from the Swiss National Science Foundation (nos. 31-62025.00 and 31-64792.01).

References

Anstis S (1995) Aftereffects from jogging. Exp Brain Res 103:476–478

Chen XY, Wolpaw JR (1995) Operant conditioning of H-reflex in freely moving rats. J Neurophysiol 73:411–415

Chen XY, Wolpaw JR (1997) Dorsal column but not lateral column transection prevents down conditioning of H-reflex in rats. J Neurophysiol 78:1730–1734

Chen XY, Chen L, Wolpaw JR (2000) The corticospinal tract in development and maintenance of H-reflex operant conditioning in rats. J Soc Neurosci Abstr 26:2206

De Leon RD, Hodgson JA, Roy RR, Edgerton VR (1998) Locomotor capacity attributable to step training versus spontaneous recovery after spinalization in adult cats. J Neurophysiol 79:1329–1340

Dietz V (1997) Neurophysiology of gait disorders: present and future applications. Electroencephalogr Clin Neurophysiol 103:333–355

Dietz V, Colombo G, Jensen L (1994) Locomotor activity in spinal man. Lancet 344:1260–1263

Dietz V, Colombo G, Jensen L, Baumgartner L (1995) Locomotor capacity of spinal cord in paraplegic patients. Ann Neurol 37:574–582

Edgerton VR, Roy RR, Hodgson JA, Prober RJ, De Guzman CP, De Leon R (1992) Potential of adult mammalian lumbosacral spinal cord to execute and acquire improved locomotion in the absence of supraspinal input. J Neurotrauma 9 (Suppl 1):S119–S128

Erni T, Colombo G (1998) Locomotor training in paraplegic patients: a new approach to assess changes in leg muscle EMG patterns. Electroencephalogr Clin Neurophysiol 109:135–139

Erni T, Dietz V (2001) Obstacle avoidance during human walking: learning rate and cross-modal transfer. J Physiol 534:303–312

Evatt ML, Wolf SL, Segal RL (1989) Modification of human spinal stretch reflexes: preliminary studies. Neurosci Lett 105:350–355

Meyer-Lohmann J, Christakos CN, Wolf H (1986) Dominance of the short-latency component in perturbation induced electromyographic responses of long-trained monkeys. Exp Brain Res 64:393–399

Myklebust BM, Gottlieb GL, Agarwal GC (1986) Stretch reflexes of the normal human infant. Dev Med Child Neurol 28:440–449

Nielsen J, Crone C, Hultborn H (1993) H-reflexes are smaller in dancers from the Royal Danish Ballet than in well-trained athletes. Eur J Appl Physiol 66:116–121

Patla AE, Prentice SD (1995) The role of active forces and intersegmental dynamics in the control of limb trajectory over obstacles during locomotion in humans. Exp Brain Res 106:499–504

Patla AE, Vickers JN (1997) Where and when do we look as we approach and step over an obstacle in the travel path? Neuroreport 8:3661–3665

Prokop T, Berger W, Zijlstra W, Dietz V (1995) Adaptational and learning processes during human split-belt locomotion: interaction between central mechanisms and afferent input. Exp Brain Res 106:449–456

Segal RL (1997) Plasticity in the central nervous system: operant conditioning of the spinal stretch reflex. Top Stroke Rehabil 3:76–87

Van Hedel HJA, Biedermann M, Erni T, Dietz V (2002) Obstacle avoidance during human walking: transfer of motor skill from one leg to the other. J Physiol 543:709–717

Wolpaw JR (1997) The complex structure of a simple memory. Trends Neurosci 20:588–594

Wolpaw JR, Dowman R (1988) Operant conditioning of primate spinal reflexes: effect on cortical SEPs. Electroencephalogr Clin Neurophysiol 69:398–401

Wolpaw JR, O'Keefe JA (1984) Adaptive plasticity in the primate spinal stretch reflex: evidence for a two-phase process. J Neurosci 4:2718–2724

Wolpaw JR, Tennissen AM (2001) Activity-dependent spinal cord plasticity in health and disease. Annu Rev Neurosci 24:807–843

Wolpaw JR, Braitman DJ, Seegal RF (1983) Adaptive plasticity in the primate spinal stretch reflex: initial development. J Neurophysiol 50:1296–1311

Zehr EP, Stein RB (1999) What functions do reflexes serve during human locomotion? Prog Neurobiol 58:185–205